The giant squid *Architeuthis*: An emblematic invertebrate that can represent concern for the conservation of marine biodiversity

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ABSTRACT

The current public perception is that there is little reason for concern for the conservation of marine invertebrates, in part due to the scarcity of emblematic species to represent that diverse group. This paper shows that giant squid can be considered an emblematic species to represent concern for the conservation of marine invertebrate biodiversity because it satisfies all the requirements of an emblematic species. It shows that *Architeuthis* attracts public interest and attention and can serve as an indicator of oceanographic conditions and ocean climate change. It asserts that *Architeuthis* can represent concerns for vulnerable marine ecosystems associated with submarine canyons and that it belongs to a broad diverse phylogenetic group of organisms associated with these canyons, sharing common concerns with that group with respect to vulnerability and conservation. This study also advocates that the giant squid can serve as an indicator of effects of ecosystem stress resulting from anthropogenic effects including ocean acidification and warming. It is also shown to be vulnerable to such anthropogenic effects as fishing, acoustic seismic exploration and, possibly, pollutants.

Key words: Giant squid, *Architeuthis*, submarine canyons, ecosystem health, conservation.

1. Introduction

The total number of marine species (invertebrates and vertebrates) is unknown to even an order of magnitude, with estimates ranging from 178,000 to more than 10 million species (Salas and Knowlton, 2006). The largest estimate was based on an extrapolation of benthic macrofauna (Grassle and Maciolek (1992). However, Briggs (1994) argued that these enormous estimates are excessive extrapolations from small samples, and May (1994) suggested instead a total of 500,000 living marine species. The new World Register of Marine Species (WoRMS, www.marinespecies.org) contains about 122,500 validated marine species names. However, leading WoRMS experts independently estimate that about 230,000 marine species are known to science. They also believe that there are three times as many unknown (unnamed) marine species as known, for a grand total on Earth that could surpass 1 million, and that the majority of them are invertebrates (Census of Marine Life. 2009. *www.coml.org*).

Invertebrates comprise the greatest component of animal diversity; representing almost 95% of all known species, and about 92% of marine species (CBC, American Museum of Natural History; http://cbc.amnh.org/center/programs/inverts.html; Bouchet, 2006). However, most cultures generally perceive the importance of conservation of marine fauna as being limited to such mega-charismatic animals as marine mammals and sea turtles (Hutchings and Ponder, 2003). The current failure to appreciate the importance of conservation of marine invertebrates is due to our ignorance of marine biodiversity, especially when compared with our knowledge of terrestrial biodiversity. Invertebrates embrace a much greater phyletic diversity and size range in the marine realm than in the terrestrial environment (Hutchings and Ponder, 2003; Bouchet, 2006; Sala and Knowlton, 2008). Also, marine invertebrates play a key role in nutrient cycling in that they are essential for the breakdown of organic matter. They form the basis of many food chains, provide habitat for other species (e.g., coral reefs), and regulate populations of other organisms through predation, parasitism and herbivory.

Furthermore, throughout the history of humankind, many marine invertebrates have been commercially harvested because of their pharmaceutical and food value (Ponder et al., 2002).

Most of the known macroscopic marine invertebrate species belong to coastal ecosystems and benthic habitats. Most uncertain is the biodiversity of pelagic ecosystems, especially in deep sea waters, which encompasses more than 90% of the aquatic biosphere. Studies of these bathy-pelagic ecosystems utilizing new technologies (Vecchione et al., 2001; Robison, 2004), together with studies of the almost virgin coastal ecosystems from the tropical Indo-Pacific Ocean, and the efforts of The Census of Marine Life global network have resulted in the discovery and description of about 3000 new marine species in 2007 (excluding prokaryotes and Protozoa) (SOS, 2009). The Census of Marine Life was conducted by researchers in more than 80 nations engaged in a 10-year scientific initiative.

Marine invertebrates (except corals) have failed to attract public or political attention and hence legislative protection. This is despite the recognized ecological importance of marine invertebrate communities and the importance of preserving the biodiversity of marine ecosystems (Worm et al., 2006). Any protection afforded to marine invertebrates has generally been by default (Hutchings and Ponder, 2003). This relative lack of interest resulted from several studies and reports, which concluded that marine invertebrates are not really threatened, or that they are less endangered than vertebrates (Templado, 2004). This perception (that marine invertebrates are relatively invulnerable) is largely based on the high reproductive capacity of some species. However, little is known about systematics, biology and ecology of most marine invertebrates, which are crucial to determining vulnerability of any species, and this ignorance further fosters public apathy. This is paradoxical, because the lack of knowledge creates great uncertainty as to how any species may respond to natural or anthropogenic perturbation. Furthermore, the capacity of any population to recover from such perturbation will depend on vital rates such as growth, maturation, fecundity and natural mortality. A final factor contributing to this lack of public interest is the scarcity of flagship or emblematic species, which could be defined as any single species of wildlife that is identified to represent the biological needs of other wildlife in the area in a conservation strategy (Parks Canada, www.pc.gc.ca). The requirements of an emblematic species include that it represents a broad group of organisms and that it shares common concerns with these organisms with respect to conservation and vulnerability to ecosystem perturbation and stress. Conservation of such emblematic species also benefits numerous lesser known species, and it serves as a bioindicator of the general state of their natural habitat as well as its conservation, especially within the most threatened ecosystems. Finally, the most important requirement is that these emblematic species be capable of focusing public and media attention.

The purpose of this paper is to determine whether the giant squid (*Architeuthis*) can be considered an emblematic species to champion the concerns for marine invertebrate biodiversity. Although *Architeuthis* is a genus comprised of an unknown number of valid species (Guerra et al., 2006) we will refer to it as a single species throughout the paper. We address the above-stated objective by evaluating the extent to which the giant squid meets the four criteria required of an emblematic species: (i) attracting public attention, (ii) serving as a bioindicator of environmental conditions, including ocean climatic change, (iii) representing a specific ecosystem, and (iv) serving as an indicator of some ecosystem stress.

2. *Architeuthis* attracts public interest

It is generally well known that marine invertebrates do not attract public interest. However, giant squids represent a notable exception, having received special attention from the middle of the last century in many national and international fora. Based on very old legends (Ellis, 1999; Heuvelmans, 2003), giant squid have become an icon or symbol that may serve to attract public interest to the issue of conservation of marine ecosystems and of marine invertebrate biodiversity in particular. Currently about 30 giant squid (*Architeuthis*) are preserved and exhibited at museums and aquaria around the world and eager visitors to these exhibits increase every year. Public interest also is reflected in the increase in sales of books on this subject, as well as in the significant recent investments in research cruises searching for live giant squids that have been supported by private and public institutions (Roper, 1999; Boyle and Rodhouse, 2005; Guerra et al., 2006; Guerra and González, 2009). Further evidence of increasing public interest includes the number of live dissections on TV and websites (e.g., www.museumvictroria.com.au/giantsquid), as well as the development of new techniques to preserve giant squids (plastinate technique applied to a specimen on display in the Paris Museum since 2008 and 3M Novec Engineered Fluid preserves two giant squid at the Smithsonian's National Museum of Natural History, Washington D.C.). Public interest has been especially promoted recently by the first photographs of live giant squid in nature and the first observations of *Architeuthis* behaviour (Kubodera and Mori, 2005). The enormous interest in this enigmatic marine mollusc is reflected in the increasing number of articles in newspapers, popular science magazines and mainstream scientific journals (Roper and Boss, 1982; O´Shea, 1997, 1999; Ellis, 1998; Soriano, 2003; Guerra et al., 2006), as well as the considerable number of visitors to web pages that contain information on giant squids (e.g., www.tonmo.com in New Zealand; www.cepesma.com in Spain, http://www.mnh.si.edu/natural_partners/squid4/ in the Smithsonian Institution, USA). A recent example of the giant squid attractiveness was the prominence of *Architeuthis* studies in national and international scientific fora dedicated to the analysis of the consequences of the effects of noises provoked by humans in marine environments. Until recently, these studies were limited to the impact of this acoustic pollution on vertebrates, particularly marine mammals (Anonymous, 2002; Guerra et al., 2004b, 2004c; Guerra and González, 2006; OSPAR, 2007; Payne et al., 2008).

Another recent example of the attraction that the giant squids draw from the public has been the opening (12th August 2010) of the "Centre of the Giant Squid" in Luarca (Asturias, Spain). This centre, funded by public and private institutions, houses a public exhibition that includes eleven specimens of *Architeuthis dux,* of various sizes, as well as three deep-sea hooked squid *Taningia danae,* including the largest specimen captured to date (124 Kg) (González et al., 2003). In this centre, without world-wide precedent, the giant squids are being used as a vehicle for educating and sensitizing the public on the need of protection and conservation of this species and the associated deep-sea marine ecosystems. The exhibition was visited by 14,000 persons in summer 2010 (http://www.cepesma.org/).

It may be argued that a species which is only rarely seen washed-up dead and damaged on the sea shore, almost never captured alive, and only once filmed alive, can be of little value as an indicator of anthropogenic effects in the ocean. However, this study has shown that there has been a clear increase in the frequency of captures in fishing trawls, since the expansion of deep-sea trawler fisheries (Table 1). Also it has been clearly shown that mortalities on beaches of Newfoundland are significantly associated with elevated water temperatures that can be expected from continued global warming and also that mass standings were associated with acoustic surveys for petroleum resources. Furthermore, it is primarily the mystery associated with the rarity of *Architeuthis* sightings that attracts public attention, making this species an excellent tool to interest the general public in the conservation of global marine biodiversity.

3. *Architeuthis* is an indicator of ocean climate change

3.1 Ocean acidification

The ongoing chemical changes in the oceans caused by increases in the concentration of CO_2 in the atmosphere include a decrease in pH, resulting from an increase in dissolved CO_2

(The Royal Society, 2005; Solomon et al., 2007). Increasing partial pressure (pCO2) in the surface ocean causes major shifts in seawater carbonate chemistry and is likely to reduce pH by 0.2–0.4 units over the course of this century (Caldeira and Wickett, 2005). Such acidification could provoke a reduction in the concentration of carbonate ions, and an increase in bicarbonate ions. That would affect marine organisms, particularly those that make the aragonite form of $CaCO_3$ in shells and plates, such as corals, coralline algae, foraminifera, coccolithophores, crustaceans and some cephalopod species of the family Sepiidae for which calcification rates may decrease by 0–56% (The Royal Society, 2005; Kleypas et al., 2006). Although *Architeuthis* lacks a calcium carbonate shell, as is true for most cephalopods, its equilibrium receptors (statocysts) have small structures made of aragonite with an organic matrix in the macula/statolith/statoconia system (Budelmann, 1996). Statoliths serve an essential role as acceleration receptors or detectors of multidimensional movement (Arkihipkin and Bizikov, 2000), and also they are “black boxes” or life-history recorders in squid (Arkihipkin, 2005). The whole system of equilibrium and balance becomes seriously affected if statolith formation is impaired due to ocean acidification. This would result in the giant squid becoming disoriented due to disruption of sensory information. These moderately active, buoyant cephalopods (Hanlon & Messenger, 1996), when disoriented, likely would float toward the surface, moving from deep cold waters to warmer epipelagic waters. Giant squids may suffocate from arterial desaturation when such increased ambient temperatures are experienced. A more than fourfold decrease in oxygen affinity of haemocyanin has been reported in one live giant squid caught near Bergen (Norway) when temperature increased from 6.4 to 15ºC (Brix, 1983; Brix et al., 1989). More recently, Brix et al., (1994) showed that the limiting P_{50} (partial pressure of oxygen in the blood needed to saturate *Architeuthis* haemocyanin to 50%), or oxygen affinity, is reached at a temperature below 10º C. However, the cause of death of this specimen is uncertain as it was moribund when found, far removed from its natural habitat in costal shallow waters.

New data are emerging on the disturbances to physiological processes in marine species such as growth, development, metabolism, osmoregulation and acid-base balance under elevated temperature and pCO2 (Fabry et al., 2008; Pörtner, 2008). In physiological terms, cephalopods are complex organisms with an active lifestyle and high levels of performance, e.g. high metabolic and growth rates (Pörtner et al., 1994). Moreover, recent studies on the responses of cephalopods and top oceanic predators to increasing temperature and pCO2 (Melzner et al., 2007; Rosa and Seibel, 2009) found that their low oxygen-carrying blood protein rendered them highly vulnerable to effects of global warming and ocean acidification. Indeed, oxygen affinity of cephalopod haemocyanin decreases with decreasing pH (Bridges, 1994) and increasing temperature (Zielinski et al., 2001), consequently reducing their metabolic scope. In this context, increasing pCO2 in seawater could impact both the cephalopod egg structure and embryonic development (Gutowska et al., 2008). Moreover, it is widely accepted that early life stages may be particularly sensitive to high pCO2 (Pörtner and Farell, 2008) especially in invertebrates (Kurihara, 2008; Dupont and Thorndyke, 2009).

3.2. Ocean temperature change

Increasing atmospheric CO_2 may have important consequences for the Earth's climate, leading to an average warming of 3ºC at the Earth's surface over the course of this century (Solomon et al., 2007). Similar trends are expected for surface ocean temperature due to the warming of the surface mixed layer (Levitus et al., 2005). Observations since 1961 show that the average temperature of the global ocean has increased to depths of at least 3000 m and that the ocean has been taking up over 80% of the heat being added to the climate system (IPCC, 2007). The giant squid may serve as an indicator of future warming of the world's oceans.

Since the late 19th century most of the specimens from the Northwest Atlantic were found stranded or floating (Table 1), and most of these were concentrated along the east coast of the small island of Newfoundland, Canada (Fig. 1), particularly during autumn (Aldrich, 1968, 1991). We found that the annual incidence of giant

- **Insert Table 1 and Fig. 1**

squid specimens in Newfoundland since 1946 was directly associated with mean autumn bottom temperature off the Newfoundland coast (Fig. 2; Spearman's correlation coefficient, $p<0.05$).

- **Insert Fig. 2**

We hypothesize that cold water on the continental shelf normally represents a barrier to giant squid distribution, but that barrier breaks down during autumn of particularly warm years. Near-bottom temperatures in such warm years, particularly in deep channels, may increase to about 3-5°C, enhancing the probability of giant squid straying onto the shelf. We agree with Aldrich (1991) who suggested that the Labrador Current plays an important role in advecting specimens (alive or dead) to the Newfoundland coast where they have been found or captured by fishermen. Live specimens would encounter seasonally warm shallow or near-surface waters in coastal areas and embayments, resulting in death due to suffocation, as noted above.

4. *Architeuthis* represents a particular ecosystem

Architeuthis has been recorded worldwide (Fig 1), with a total number of 677 specimens recorded since the 16th century (Table 1). It has been especially frequent in the marine areas of the Southwest Pacific around New Zealand and Tasmania (183 specimens), the Northeast Atlantic, especially off northern Spain (152) and Newfoundland (148); and the Southeast Atlantic (Namibia and South Africa) (>60) (O'Shea 1997; Ellis 1998, Förch, 1998, Sweeney and Roper 2001, González et al., 2002; Guerra et al. 2004a; Guerra et al., 2006; O'Shea and Bolstad, 2008).

We examined the relationship between the number of recorded specimens and some of the main characteristics of the areas. The results (Table 1) showed that *Architeuthis* appears mostly in areas with submarine channels or canyons that cut transversally across the continental shelf. These features provide suitable habitat, including high productivity, in close proximity to shallower fishing grounds. The presence of predators (mainly sperm whales) represented one of the main explanatory variables. This is not surprising due to the close association of giant squids with sperm whales through a prey-predator relationship (e.g., Clarke, 1980). The bottom topography of the regions of highest incidence of giant squid records (Fig. 1) share one common characteristic: abyssal-depth plains meet shallower continental shelves, with confined deep channels and canyons in the plain-shelf border. Other regions of the world's oceans, with low incidence of giant squid sightings, do not feature deep channels or canyons (Guerra et al., 2006).

These deep canyons generally support a high biodiversity and represent vulnerable marine ecosystems (VMEs). The European Commission has defined VMEs as "any marine ecosystem whose specific structure and function is, according to the best scientific information available and to the principle of precaution, likely to be compromised by stress resulting from physical contact with bottom gears in the course of fishing operations, including inter alia reefs, seamounts, hydrothermal vents, cold water corals or cold water sponge beds" (EC, 2007). We illustrate the characteristic high biodiversity and vulnerability of canyons based on our own research in Avilés's canyon, off Asturias; northern Spain (Fig. 1), Avilés's canyon is one of three canyons that collectively represent a portion of the commercial offshore fishing ground. Located 7 miles off the coast, this large submarine canyon represents one of the most remarkable ecosystems on the Bay of Biscay platform, with depth increasing from 220 m depth over the shelf to 4,750 m down the slope. Investigations using ROVs (remotely operated vehicles) to depths of 600 m found large colonies of deep cold-water white corals (*Madrepora oculata*), draping the hillsides of the canyon beyond 200 m depth and being especially dense on the ledges. Other corals included many gorgonian colonies of various species and black corals (*Parantiphates hirondelle*, *Anthipates subpinnata* and *A. dichotoma*), which are included in Annex II of the Convention on International Trade in Endangered Species (CITES). Glass sponges (*Rosella* spp) also represented a component of the previously little-known rich and diverse fauna centred in this zone (Oceana, 2009).

Our recent investigations showed that the Avilés's canyon ecosystem provides essential habitats for reproduction of important commercial species. Although fishing effort in this zone has not increased in the last 5 years, available time-series data (Laria unpublished data) show that some species previously considered rare are becoming more common, including the oarfish (*Regalecus glesne*), the ocean moonfish (*Lampris guttatus*), Krøyer's deep sea anglerfish (*Ceratias holboelli*) and the unicorn filefish (*Aluterus monoceros*). Some of these species, like *A. monocerus*, are not specifically reported to be endemic to the Bay of Biscay waters, but it is rather a tropical species. We also found an increased abundance of some species due to northward extension of their distributional limit in the eastern Atlantic, including the puffer (*Lagocephalus lagocephalus),* Loppe's tadpole fish (*Ijimaia loppei*) as well as the rhomboid squid (*Thysanoteuthis rhombus*). The last updated checklist of fish species in Galicia waters (NW Iberian Peninsula), adjacent to Asturian waters, showed that fish species of African origin increased notably in the last ten years, now accounting for 4.3 % of the 398 species recorded for this zone, which is included in the Lusitanic Biogeographical Province (Bañón et al., 2010). A tropical poikilothermic species, the paper nautilus (*Argonauta argo),* has also recently been recorded in this area (Guerra et al., 2002a). These new records may be related to the increases in sea surface temperature observed off the Galician coast (0.8º C in the last ten years).

Aviles's canyon also provides habitat for large fishes such as swordfish (*Xiphias gladius*) and various species of tunas and sharks, which are exploited by fisheries as either targeted or incidental catches (INDEMARES, 2009. http://www.indemares.es). Among sharks, the most important species are the harvest shortfin mako (*Isurus oxyrinchus*), blue shark (*Prionace glauca*) and smooth hammerhead (*Sphyrna zygaena*), all of which are predators of the giant squid (see Guerra et al., 2006 and Guerra and González, 2009 for reviews). The shortfin mako and smooth hammerhead are classified as vulnerable in the IUCN Red List of Threatened Species.

A diverse community of marine mammals is distributed around Avilés canyon, The most abundant odontocetes are the common, striped and bottlenose dolphins (*Delphinus delphis*, *Stenella coeruloalba* and *Tursiops truncatus,* respectively), the long finned pilot whale (*Globicephala melas*), Cuvier's beaked whale (*Ziphius cavirostris*), and the sperm whale (*Physeter macrocephalus*) (INDEMARES, 2009; Lens et al., 2006). These predators share the habitat with the emblematic giant squid (*Architeuthis dux*), which has been found in the stomach contents of the toothed whales species, but not in dolphins (Santos et al., 2002; also see Guerra et al., 2006 and Guerra and González, 2009 for reviews). The majority of these species are classified as vulnerable in the IUCN Red List of Threatened Species.

Since giant squid records are associated mostly with submarine canyon ecosystems, which have been selected as National Marine Sanctuaries in many world oceanic areas, we conclude that *Architeuthis* serves to raise social awareness for the conservation of a diverse group of organisms that inhabits these canyons. It also shares common concerns with that group with respect to vulnerability and conservation of sensitive and threatened ecosystems. The Gully submarine canyon on the Nova Scotian Shelf (Fig 1) and Monterey canyon in Monterey Bay (Ca, USA, Fig.1) represent two clear examples of VMEs (Hooker et al., 1999; Mortensen and Buhl-Mortensen, 2005; Deans and Rigsby, 1999). Also, the Spanish Ministry of

Environment is studying a proposal for declaring Avilés's canyon together with the Cap de Creus submarine canyon in the Western Mediterranean (Fig.1) as protected marine areas, due to their unique oceanography, sedimentary and geomorphic features, as well as other ecosystem characteristics, which include a great variety of habitats that contain an impressive diversity of organisms that share a potentially high vulnerability to a variety of human activities.

Any submarine canyon is a complex ecosystem where many communities coexist and multitrophic interactions and intricate food webs are extant. Despite the wealth of research on pairwise species interactions (Tylianakis et al., 2008a), understanding the response of any species to ecosystem perturbation presents inherent challenges and needs to consider the real-world complexity of effects of interactions involving a diversity of species (Tylianakis et al., 2008b). This kind of research requires new approaches that explicitly take large-scale, spatio-temporal variability into account, even in the case of complex interaction networks (Laliberté and Tylianakis, 2010). It also must consider direct and indirect multitrophic interactions and the increasing evidence for nonlinearities and (synergistic or antagonistic) interactions among many global drivers of ecosystem structure (Tscharntke and Tylianakis, 2010). Deriving management strategies in the face of multiple drivers to address biodiversity conservation and/or ecosystem preservation is difficult, and understanding the combined effects of threats that can affect an entire community is an enormous challenge. Therefore, further multidisciplinary and global studies should be carried out in order to obtain a better understanding of the role of giant squid in the ecosystems they inhabit.

5. *Architeuthis* is an indicator of ecosystem stress

5.1. Indicator of climate change

We have already described how *Architeuthis* can represent an indicator of the state of the ocean climate and effects of climate change, with respect to changes in ocean acidification and temperature. Therefore it represents an indicator of ecosystem stress due to anthropogenic greenhouse gas emissions and associated global ocean warming and acidification.

5.2. Indicator of effects of acoustic waves produced during seismic surveys

Stranding events of giant squid on the northern coast of Spain (Asturias) generally reflect one or two specimen per year (Table 2). However, this pattern changed in autumn 2001 when five very large giant squids were found stranded in a localized area within a single month (Table 2) (Guerra et al., 2004 c).

- **Insert Table 2**

Two years later a similar event occurred when four animals were found floating or stranded along the Asturian coast during a single week of September 2003 (Table 2). We did not find an obvious cause of death in any of these giant squid, which ranged 60-200 kg in weight and 7-12 metres in total length. However, internal examinations showed that two of the squids suffered extensive damage to internal muscle fibres, their stomachs were ripped open and their digestive tracts were mangled. One animal in particular probably had died from its injuries. Some of the squids had also suffered severe damage to their statocysts that would have effectively disorientated them (Guerra et al., 2004 c). Coincidentally, at the time of both mass strandings, vessels had been conducting seismic geophysical surveys in the vicinity, using ten compressed air guns that produced sound waves of low frequency (below 100 Hz) and high intensity (SL=240 dB re 1 μPa at 1m per airgun). Statocysts may play an important additional role in low frequency sound reception (Hanlon and Budelmann 1987; Kaifu et al., 2008; Hu et al. 2009; Mooney et al., in press).

Currently, very little is known about the impact of marine acoustic technology on cephalopods (Anonymous, 2002; André et al., 2010). However, our hypothesis is consistent with the strong behavioural reaction of one squid species (*Sepioteuthis australis*) to airgun sound in controlled exposure experiments. That squid showed an increase in alarm responses above 156 dB_{RMS} re 1 µPa. Squid quickly changed direction away from the airgun and, in many cases, expelled ink. Discharge of ink sacs was not evident if the array output gradually increased as opposed to a full volume report (McCauley et al., 2000). Most importantly, recent studies carried out by M. André and coworkers of the Laboratory of Applied Bioacoustics, Technical University of Catalonia (Spain) showed, for the first time, evidence of acoustic trauma in the sensory hair cells of the statocysts of several cephalopod species under low frequency sound in controlled experiments (André per. comm. October, 2010). Therefore, besides causing disorientation and physical damage, acoustic waves from the air guns could also have dazed the giant squid. Disoriented and dazed, these moderately active, buoyant cephalopods could have floated towards the surface, moving from deep cold waters to warmer and shallower waters, where they died due to the physiological mechanism of oxygen desaturation previously described (Guerra et al., 2004c; Guerra and González, 2006).

Recently, we found additional circumstantial evidence of the threat represented by seismic exploration. Two stranded giant squid specimens (male and female) were found in December 2004 in Newfoundland waters within two well-separated east coast bays, within a 17 day period (Dawe, unpublished data), only 3 months after the first seismic survey of Orphan Basin, a deep slope area almost enclosed by shallower shelf and ocean currents. This association is less convincing than those at Asturias, because the 2004 Newfoundland strandings also were associated with high bottom temperature (Fig. 2), which, as previously noted, increased the probability of giant squid strandings in that year.

Further investigation is needed into the physical, physiological and behavioural effects of high-intensity acoustic pulses on cephalopods, as well as on other deep-water organisms, including the relationship of these effects to tissue and organ lesions and to mortalities. As has been shown for cetaceans and sonar (Jepson et al., 2003), these findings should be considered in a broader conservation sense, to evaluate whether the regulation and limitation of acoustic pulses is advisable to limit such anthropogenic effects on cephalopods and other deep-sea organisms. A precautionary approach would require that until evidence of environmental impact is sufficient to warrant a ban on application of high energy and low frequency marine acoustic technology, mitigation strategies involving survey design, timing, ramping of source levels and prohibited zones should be implemented (Anonymous, 2002; André et al., 2010).

5.3. Indicators of effects of deep-water fisheries

The world records of *Architeuthis* due to commercial fishing represent about 29 % of the total records (Table 1). However, this is likely an underestimate because, at least in the waters off northern Spain, an unknown but high percentage of the findings registered in the 1970s as floating or stranded (SF, Table 1) were actually alive when captured by trawlers but were discarded and subsequently observed either floating at the surface or stranded on the coast. This, together with the high incidence of records from deep-sea fisheries (Table 1), suggests that fishing represents the main threat for *Architeuthis*. This is a great concern since overfishing is becoming increasingly important in all oceanic ecosystems (Coll et al., 2008), and the shift from shelf to deep-sea fisheries is depleting populations of long-lived and late-maturing species, which recover very slowly (Devine et al., 2006).

An example of the effects of fishing due to relatively deep-sea fisheries is seen in the Carrandi fishing ground off northern Spain (Fig. 1). The absence of *Architeuthis* records in this area from 2006 to 2008 (Table 2) coincided with cessation of most fishing activity, particularly for blue whiting (*Micromesistius poutassou*), during this period. However, giant squid specimens were captured again when this fishery resumed in 2009 (Table 2). Otter trawlers and pair trawlers transversally cross the steep slope of Avilés's canyon at depths ranging 250-700 m. Each haul, of 8-10 hours duration, features repeatedly raising and lowering the trawl gear, depending on bottom topography and fish distribution.

5.4. Indicators of pollutant impacts

Cephalopods play a key role in marine ecosystems both as predators and prey. They constitute a class of marine molluscs which are found in a great variety of habitats from coastal waters to very deep-ocean environments (Boyle and Rodhouse, 2005). Independently of the species, habitat or life span, cephalopods share the ability to accumulate inorganic and organic pollutants such as metals, PCBs or organochlorine pesticides (e.g. Bustamante et al., 2006 a, b; Seixas and Pierce, 2005; Storelli et al, 2005; Ueno et al., 2003, Yamada et al., 1997). Bustamante et al., (2008) showed that, as for 25 other families of cephalopods, the digestive gland and the branchial hearts of *Architeuthis* had higher concentrations of Ag, Cd, Co, Cu, Fe, Ni, Se, V and Zn, than any other organs, highlighting their major role in the bioaccumulation and detoxification processes. With the exception of Hg, the muscles of these specimens, from the Mediterranean and Atlantic Spanish waters, showed relatively low trace element concentrations. Nevertheless, this tissue contained the main proportion of the total As, Cr, Hg, Mn, Ni, and Zn body burden because muscles represent the main proportion of the squid mass. These findings suggest that the metal metabolism is overall the same as for other cephalopod families from neritic waters. In females, Zn concentrations increased in the digestive gland with the squid's weight, likely reflecting physiological changes during sexual maturation. Comparing the trace element concentrations in the tissues of *Architeuthis*, higher Ag, Cu, Hg and Zn concentrations in the squid from the Mediterranean than in those from the Bay of Biscay reflected different exposure conditions. Higher Cd concentrations in the digestive gland of *Architeuthis* than in that of other meso-pelagic squids from the Bay of Biscay, suggest that *Architeuthis* may feed on more contaminated prey or that it has a longer life span that other cephalopods.

Lacoue-Labarthe et al., (2008) hypothesized that, in coastal shallow waters, ocean acidification and warming could affect embryonic metabolism and the shielding properties of the eggshell components, and could lead to shifts in a) the accumulation of an essential element (Zn) and b) the capacity of the eggshell to protect against the penetration of non-essential or toxic elements, such as Ag and Cd, known for their contrasting up-take behaviours. Controlled experiments have demonstrated strong and contrasting effects of pH and temperature on the bioaccumulation of several metals in cuttlefish *(S. officinalis)* eggs and embryos (Bustamante et al., 2006b). In the context of the ocean acidification, it appears that decreasing pH to 7.85 should lead to some possibly beneficial effects, such as a larger egg (and presumably hatchling) size and a better incorporation of essential elements such as Zn in the embryonic tissue. This may increase survival of newly hatched juveniles. Moreover, the incorporation of a toxic metal such as Cd (unpublished data) in the embryonic tissue decreased with increasing pCO2 whereas the accumulation of Ag was strongly enhanced under acidified conditions. According to these initial results, further work is now warranted to better assess the ecotoxicological consequences of combined climate change effects, including effects of an increased level of anthropogenic coastal pollutants on cuttlefish egg development and the recruitment success of juveniles into their populations (Lacoue-Labarthe et al., 2009). It is also noteworthy that increasing pCO_2 in seawater leads to metabolic depression in marine organisms due to changes in their acid-base balance (e.g. Portner et al., 2004; Portner, 2008). Indeed, due to the high Bohr coefficient of their haemocyanins, cephalopods showed reduced aerobic scope under elevated pCO_2 in seawater and also showed a high sensitivity to hypercapnia (Portner et al., 2004; Melzner et al., 2007). It follows that the reduced metabolic rates (Rosa et al., 2009) of eggs under acidified conditions limited embryonic growth.

It might be argued that these effects of pollutants on various species and developmental stages of cephalopods are only valid for coastal waters, where the pollution can be particularly severe. However, recent studies in relation to the oil spill in the Gulf of Mexico, which flowed for three months in 2010, identified oil plumes in the deep waters of that zone, including one as large as 16 km long, 4.8 km wide and 91 m thick. The shallowest oil plume the group detected was at about 700 m, while the deepest was near the seafloor at about 1,400 m (http://www.noaanews.noaa.gov/stories2010/20100506_spillsampling.html).

NOAA researchers, reporting on separate studies carried out by the Universities of South Florida and Princeton confirmed that the subsea plumes of oil resulted from the Deepwater Horizon. They also concluded that the deep plumes of dissolved oil and gas will likely remain confined to the northern Gulf of Mexico and that the peak impact on dissolved oxygen will be delayed (several months) and long lasting (years) (ProPublica, 2010; Adcroft et al., in press).

The ecological impact of this disaster is almost incalculable. However, a comprehensive 2009 inventory of offshore Gulf species numbered 15,700. The area of the oil spill includes 8,332 species, including more than 1,200 fish, 200 birds, 1,400 molluscs, 1,500 crustaceans, 4 sea turtles, and 29 marine mammals (Biello, 2009). In addition, some specimens of bottom-dwelling pancake batfishes (recently revised *Halieutichthys aculeatus* species complex) in the Gulf of Mexico (Ho et al., 2010), which inhabit a subtropical, sandy, reef-associated, and 45–820 m deep environment, were found to be engulfed by the oil spill (Science Daily, 2010).

The finding of oil plumes in the deep waters in the Gulf of Mexico demonstrates that deep-sea ecosystems are not spared from global contaminant distribution. Habitat of adult *Architeuthis* is submarine canyons. Submarine canyons, in particular nearshore ones, serve as a sedimentary trap enhancing the accumulation of organic and inorganic contaminants from multiple sources mainly originate at adjacent shelf (Maurer et al., 1966). Moreover, some of these habitats are zones of large oil tanker traffic, while others feature oil-producing platforms. Therefore, these habitats are highly vulnerable to effects of such pollutants and some may have already been affected by high levels of pollution. Although the location and type of spawning of *Architeuthis* are unknown (Guerra et al., 2006), the eggs are likely planktonic, as in other oegopsid squids (Nesis, 1995; Guerra et al., 2002b). The only paralarvae of giant squid captured to date were epipelagic (O'Shea and Bolstad, 2008). Therefore, embryonic development may occur in relatively shallow waters. Consequently, the giant squid may experience the effects of various types of contaminants throughout its life cycle. It may become increasingly threatened by pollutants in the future, as it has been show that ongoing ocean acidification modifies pollutant bioaccumulation rates in cephalopods (Lacoue-Labarthe et al., 2009).

Conclusions

Although it is recognized that the selection of a suitable indicator for monitoring the effects of any natural or anthropogenic change is a complex issue (Tullock et al., in press), *Architeuthis* displays all the traits required to be considered an emblematic invertebrate to represent concern for the conservation of marine biodiversity and ecosystem health. It attracts public interest and attention. It seems to be susceptible to ocean acidification and warming, and consequently it is potentially vulnerable to ocean climate change. It represents concerns for a broadly diverse phylogenetic group, as well as concerns for vulnerable marine ecosystems associated with submarine canyons. It also is vulnerable to such anthropogenic effects as fishing, acoustic seismic exploration, and possibly pollution. It is not presently possible to determine whether it is a threatened species, but the recent increases in deep-sea fishing and seismic exploration with coincident *Architeuthis* records raise concern that it may become vulnerable, if it is not already so.

It may be argued that *Architeuthis* is not representative of marine invertebrates in general due to its atypically large size and its rarity. However, its large size ensures that many mortalities are detected, public interest drawn, and concerns for conservation raised. Furthermore, it is the perceived mystery surrounding its large size and rarity that attracts such a high level of public interest, making it an ideal emblematic representative of marine invertebrates and an excellent tool for garnering public interest in the conservation of global marine biodiversity. Although *Architeuthis* is rarely encountered, the knowledge base is far more depauparate for the majority of other marine invertebrates. Given this very high level of uncertainty it would be prudent to consider marine invertebrates in general to be vulnerable to natural and anthropogenic change, and to recognize that there is reason for concern for their conservation. Furthermore, while, the population sizes of *Architeuthis* species remain unknown they have a very broad geographic range of distribution (Guerra et al., 2006). This is an asset to an indicator species in that a broad geographic range promotes representation of concerns and public awareness across a large geographic area (Tullock et al., in press), in the case of *Architeuthis* at the global scale.

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